From Fields to Landscapes: Effects of Agricultural Land Use and Landscape Heterogeneity on Farmland Birds

Matthew Hiron
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2013

Acta Universitatis Agriculturae Sueciae
2013:89

Cover: Some farmland habitats and a 25 km^2 farmland landscape
(photos: Sönke Eggers)

ISSN 1652-6880
ISBN (print version) 978-91-576-7916-1
ISBN (electronic version) 978-91-576-7917-8

Print: SLU Service/Repro, Uppsala 2013

From Fields to Landscapes: Effects of Agricultural Land Use and Landscape Heterogeneity on Farmland Birds

Abstract

Farmland biodiversity has declined because of agricultural intensification. Agri-environment schemes (AESs) seem to have limited effect in stopping and reversing declines. Reasons for this lack of effect could be: (1) failure to target important habitats, (2) the effects of schemes are strongly context-dependent, and (3) the effects are measured at the wrong spatial scale. Evidently, we still need more information about the relationships between agricultural land use and biodiversity at local and landscape scale. I investigated how patterns in habitat-specific abundance and species richness of farmland birds related to land use in 37 arable field dominated landscapes (25 km^2). The aim of the study was to establish if agricultural land uses, non-crop habitats and AESs are linked to high species diversity or abundance of birds in open plains of southern Sweden. First, I found a clear switch in crop-specific densities (from autumn- to spring-sown) of a farmland specialist species, the skylark (*Alauda arvensis)*, during the breeding season and this temporal change depended on region. Second, I found that farmsteads had higher species richness and abundance of birds compared to semi-natural pastures and infield non-crop islands. The presence of farm animals increased bird diversity and abundance at farmsteads. Furthermore, densities of non-crop nesters at farmsteads increased with increased average field size of the landscape, showing that farmsteads are especially important bird habitats in arable plains. Third, I showed that payments for AESs target important habitats for birds in the region. AESs for cultivated grasslands, semi-natural pastures and management of landscape elements with nature-culture values related positively to species richness or abundance of birds. Landscape level uptake of organic farming did show effects on local species richness depending on the composition of the landscape. Fourth, I showed that heterogeneity of crop cover at the 25 km^2 scale did not relate to species richness (with the possible exception of field-nesters in the most simplified landscapes). Total species richness of field-nesting species declined in heterogeneous landscapes with more non-crop cover. Farmland plains are important for farmland birds, but variation in species richness there can be found at the beta and gamma levels rather than at the alpha level. My study shows that, biodiversity patterns need to be considered at different spatial scales when designing and evaluating conservation management in farmland.

Keywords: Agri-environment schemes, biodiversity, intensification, mixed-farming, conservation, habitat selection, farmsteads, autumn-sown crops, semi-natural pastures, diversity partitioning

Author's address: Matthew Hiron, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: matthew.hiron@slu.se

Dedication

To my family

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hiron, M., Berg, Å. & Pärt, T. (2012). Do skylarks prefer autumn sown cereals? Effects of agricultural land use, region and time in the breeding season on density. *Agriculture, Ecosystems & Environment* 150, 82–90.

II Hiron, M., Berg, Å., Eggers, S. & Pärt, T. (2013). Are farmsteads overlooked biodiversity hotspots in intensive agricultural ecosystems? *Biological Conservation* 159, 332–342.

III Hiron, M., Berg, Å., Eggers, S., Josefsson, J. & Pärt, T. (2013). Bird diversity relates to agri-environment schemes at local and landscape level in intensive farmland. *Agriculture, Ecosystems & Environment* 176, 9–16.

IV Hiron, M., Berg, Å., Berggren, Å., Eggers, S., Josefsson, J. & Pärt, T. (2013). Linking large-scale patterns in species diversity to heterogeneity of crop and non-crop cover in agricultural landscapes. Manuscript.

Papers I–III are reproduced with the permission of the publisher.

The contribution of Matthew Hiron to the papers included in this thesis was as follows:

I Main author, fieldwork coordination, data management and analysis. Study design with Tomas Pärt and Åke Berg.

II Main author, fieldwork coordination, data management and analysis. Study design with Tomas Pärt and Åke Berg.

III Main author, fieldwork coordination, data management and analysis. Study design with Tomas Pärt and Åke Berg.

IV Main author, fieldwork coordination, data management and analysis. Study design with Tomas Pärt and Åke Berg.

1 Introduction

1.1 Biodiversity in farmland ecosystems

Agricultural land in Europe is extremely important not only for food production but also ecologically as it covers nearly 50% of the continent's surface area and half of the continent's species utilise farmland habitats (Stoate *et al.*, 2009). However, populations of a number of organism groups have declined in farmland and consequently many species are now of conservation concern (Tucker & Evans, 1997; Krebs *et al.*, 1999; Wilson *et al.*, 1999). These trends have prompted more than two decades of intensive research focusing on an important question: How can we halt and reverse population declines of farmland species? Thus, various conservation measures have been introduced to mitigate negative effects of agricultural intensification on biodiversity, but their efficacy is uncertain (Kleijn *et al.*, 2011). Agri-environmental schemes (AES, the main conservation tools in agro-ecosystems) do not appear to be providing expected biodiversity gains (Kleijn *et al.*, 2006; Whittingham, 2007, 2011) and historical land use changes, species' habitat associations and the effectiveness of conservation measures seem to vary among regions or landscape types (Wretenberg *et al.*, 2006, 2007; Whittingham *et al.*, 2007; Batáry *et al.*, 2011).

In European farmland some of the most familiar and common species have declined, notably farmland birds (Chamberlain & Fuller, 2000; Gregory *et al.*, 2005; Wretenberg *et al.*, 2006). Skylarks, lapwings (*Vanellus vanellus*), starlings (*Sturnus vulgaris*), house sparrows (*Passer domesticus*), swallows (*Hirundo rustica*) and others are all species that have followed human cultivation of the land. They forage and breed in the fields, farmsteads or remaining patches of semi-natural habitat, but populations of many of these farmland bird species have declined in large parts of Europe, in many cases by over 50% between the 1970s and 2000 (Gregory *et al.*, 2004; Wretenberg *et* *al.*, 2006). This is a cause of wider concern as birds are considered good indicators of environmental "health" because they are dependent on many other organisms for their survival, such as invertebrates and weeds (Wilson *et al.*, 1999; Gregory *et al.*, 2005). Thus, if modern farmland cannot support viable populations of common bird species that are most well adapted to the ephemeral and dynamic resources in heavily modified agricultural environments the pressures on many other species are likely to be intense (Pain & Pienkowski, 1997). Furthermore, if common species decline so do the ecosystem services they provide (Wilson *et al.*, 1999; Whelan *et al.*, 2008).

1.2 Agricultural intensification and birds

Birds that use farmland during the breeding season are a diverse group, ranging from farmland specialists that both nest and forage in agricultural fields to species that nest in non-crop habitats (such as farmsteads, woodland edges and shrubby field margins) but depend on open fields for foraging. Furthermore, a number of species that mainly breed in other biomes also use farmland, for example during migration (Dänhardt *et al.*, 2010). Therefore, these species have varied ecological needs and a number of changes have been identified in northern European agricultural areas that might be responsible for declines in populations of farmland birds (Krebs *et al.*, 1999; Stoate *et al.*, 2001; Newton, 2004; Donald *et al.*, 2006; See Butler *et al.*, 2007; Wretenberg *et al.*, 2007), for example:

- Changes in crop fields associated with efforts to raise yields, including autumn sowing, use of taller, denser and faster growing crop varieties, increased use of fertilizers and pesticides, and consequent reductions in the need for crop rotations.
- Increases in field size and losses of field margins, e.g. surface ditches and hedgerows.
- Polarisation of farming systems, e.g. the specialisation in annual crop production in some entire regions and animal husbandry in others.
- Intensification of grassland management leading to losses of semi-natural pastures, increases in grazing pressure, denser swards and more frequent mowing.
- Extensification and abandonment: loss of open farmland through ecological succession of unmanaged fields and dominance of ley farming in less productive regions.

All of these changes have synergistically reduced habitat heterogeneity in farmland (Benton *et al.*, 2003), and consequently the variety of resources available to a number of bird species that depend on it. Extensification of farming and farm abandonment have been identified as potential causes of biodiversity declines in less productive regions (Wretenberg *et al.*, 2007, 2010).

1.3 Changes in Swedish agriculture

Wretenberg *et al.* (2006) presented data on the major changes in Swedish agriculture during the last three decades of the twentieth century. This was a time period of pronounced declines in farmland bird populations (Benton *et al.*, 2002; Gregory *et al.*, 2004; Wretenberg *et al.*, 2006, 2007). Wretenberg *et al.* (2006) also showed that farmland bird populations in Sweden and the UK had similar temporal patterns although the agricultural intensification patterns differed. For example, in the UK a much discussed change in agriculture that could be causally related to the declines is a switch from predominant use of spring-sown cereals in the 1950s to almost entirely (90%) autumn-sown cereals in the 1990s (Pain & Pienkowski, 1997).

In contrast, in Sweden the area of arable land used for autumn-sown cereals did not change markedly between 1970 and 2000 although areas of both arable land and spring cereals declined. Therefore, the proportion of remaining farmland used for autumn-sown crops has increased, but certainly not to the levels in UK farmland. Changes in crop sowing time have also varied among regions in Sweden, notably autumn-sown crops account for larger proportions of cereal cover on the productive plains than in other regions (Jansson, 2011). In addition, yields (kg/ha) have increased for cereals such as autumn-sown wheat, spring-sown wheat and spring-sown barley (Fig. 1).

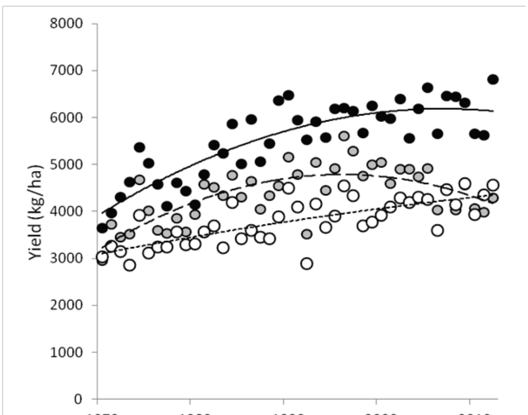

Figure 1. Changes in yield (kg/ha) in three crop types between 1970 and 2011. Black circles = autumn-sown wheat, grey circles = spring-sown wheat and open circles = spring-sown barley. Lines are fitted to aid visualisation and have not been evaluated statistically.

Furthermore, between 1970 and 2000 the area of semi-natural pastures declined from 700 000 ha to 550 000 ha in Sweden (Wretenberg *et al*., 2006), possibly because of both ecological succession to scrub or woodland and conversion to more productive, fertilized grasslands. One of the most dramatic changes in farmland has been a steep decline in the number of farm holdings with cattle, for instance between 1970 and 2000 the number of holdings with cattle in southern Sweden decreased from around 80 000 to less than 30 000 (Wretenberg *et al*., 2006).

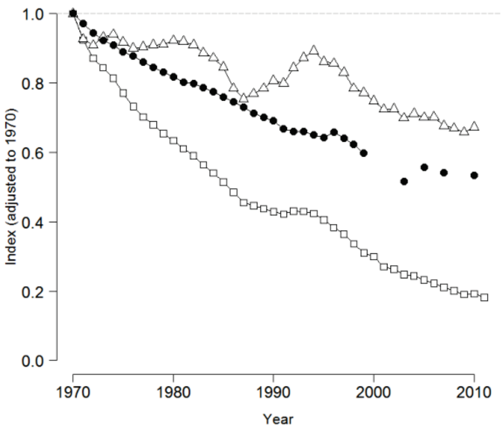

Figure 2. Changes in numbers of cattle (triangles), cattle farms (squares) and all farms (circles) in the plain regions of Götaland, Svealand and Skåne, relative to numbers in 1970 (683 778 cattle, 28 840 cattle farms and 46 611 farms) between 1970–2011.

As shown in Figure 2, the steep decline has continued to the present day. However, the number of cattle has not declined as steeply (Fig. 2). These trends suggest that stocking rates of remaining animal farms have increased, contributing to the polarisation of farming practices at both farm and landscape levels. Accordingly, between 1970 and 2000 numbers of small, medium-sized and large farm holdings (covering 2.1–20 ha, 20–50 ha and >50 ha) declined markedly from 110 000 to 40 000, less sharply from 30 000 to 20 000, and almost doubled from 10 000 to 19 000, respectively. The steep decline of small farm holdings has resulted in marked changes in farmland for three main reasons. Previously open farmland is no longer managed and becomes scrub or woodland. The same management regimes are applied to large areas of arable land or pastures, and structures associated with active agriculture (barns, paddocks, manure heaps, crop and animal feed storage facilities) disappear when farmsteads stop being used for active agriculture and are solely used as homes for people.

1.4 Nature conservation in farmland

Declines in biodiversity and environmental degradation in European farmland have led to the introduction of various AESs (including schemes to promote organic farming) intended to minimize the impact of agricultural food production on environments and farmland species of special conservation interest (Kleijn & Sutherland, 2003). All EU member countries are obliged to formulate and implement agri-environment programs (Kleijn *et al.*, 2006), which should be tailored to meet country-specific environmental threats, needs and policies (Josefsson, 2012). However, the schemes' effectiveness in promoting biodiversity appears to have been highly variable. Indeed, they have reportedly had positive, negative or no effects on various biodiversity measures (Bengtsson *et al.*, 2005; Kleijn *et al.*, 2006). They often have the clearest positive effects when conservation actions are implemented for specific species with well-established causes of declines (Aebischer *et al.*, 2000; Peach *et al.*, 2001; Vickery *et al.*, 2004) or for specific habitats where required management practices can be easily prescribed, e.g. mowing and grazing of grasslands (Batáry *et al.*, 2010).

The failure of AESs to increase biodiversity more generally has been previously discussed (Whittingham, 2007) and several contributory factors have been identified. Firstly, they may be implemented in areas where target species groups do not occur. Secondly, areas they cover may be located far away from other required habitats, thereby spatially decoupling habitats for species with multiple habitat requirements. Thirdly, AESs have reportedly had mixed effects on population-level processes and they are not always implemented at a spatial scale that benefits populations of target species (Davey *et al.*, 2010; Baker *et al.*, 2012). Lastly, but equally importantly, their effects on biodiversity differ between landscapes and regions (Whittingham *et al.*, 2007; Davey *et al.*, 2010; Batáry *et al.*, 2011).

The uncertainty regarding the effectiveness of AESs strongly indicates that every country must regularly evaluate their schemes to identify those that are effective, and the species they are promoting. For this, governments must have information on the habitats (defined in terms of land uses and landscape elements) that are important for biodiversity in farmed ecosystems, not only in semi-natural and particularly species-rich areas but also in wider landscapes dominated by intensively managed farmland.

1.5 Key knowledge gaps

Agricultural practices, land use changes and crop phenology differ among European regions and even within farming regions of the same country (Whittingham *et al.*, 2003; Wretenberg *et al.*, 2006; Báldi & Batáry, 2011). Thus, relationships between agricultural land use and biodiversity will probably be strongly context-specific, as will effects of conservation measures (Batáry *et al.*, 2011). For example, crop types that provide poor habitats in one region might be less problematic or even provide rich habitats in other regions (Whittingham *et al.*, 2003; Stoate *et al.*, 2009) due (for instance) to effects of variations in climatic or edaphic conditions on their growth and development. In addition, non-crop habitats may be beneficial for some farmland bird species (Fuller *et al.*, 2004; Herzon & O'Hara, 2007; Vepsäläinen *et al.*, 2010), but disadvantageous for others (Pickett & Siriwardena, 2011). Furthermore, the changes in agriculture that have caused declines in farmland biodiversity vary between regions (Stoate *et al.*, 2001; Wretenberg *et al.*, 2006; Báldi & Batáry, 2011).

A factor that limits our understanding of the ecology of farmland birds in simplified, intensive agricultural landscapes is that much of our knowledge is based on studies from western and central Europe. Consequently, we still lack basic information on the general habitat associations of farmland birds in the intensive agricultural regions of southern Scandinavia. For example, land uses such as cultivation of autumn-sown crops are reportedly beneficial for skylarks in Finland (Piha *et al*., 2003), but in the UK the switch from spring- to autumn-sown crops has been implicated as a major driver of skylark declines (Donald, 2004). Thus, key issues to resolve for Swedish researchers and decision-makers is whether skylarks (and other species) in Sweden prefer or avoid autumn-sown crops and whether seasonal changes in their abundance in autumn- and spring-sown croplands are similar to those in other regions (e.g. Chamberlain *et al*., 1999).

The effects of semi-natural habitats and low intensity agricultural production on biodiversity in farmland have received considerable attention (Pärt & Söderström, 1999; Henderson *et al.*, 2000; Vickery *et al.*, 2002; Batáry *et al.*, 2010; Smith *et al.*, 2010; Wretenberg *et al.*, 2010; Jonason *et al.*, 2011). However, many farmland landscapes are almost devoid of large tracts of open semi-natural habitats, and some low intensity farming practices cover only relatively small areas (statistics from this study & Jansson, 2011). However, one farmland habitat that is found in most agricultural landscapes, but has received little attention in discussions of conservation measures, is the farmstead. Farmsteads provide habitats for various species of conservation interest. However, apart from anecdotal evidence in management books, information on their value for biodiversity in intensive agricultural ecosystems is restricted to findings of a few studies that focused on small numbers of farms or single species (e.g. Blanco *et al.*, 1997; Ahnström *et al.*, 2008; Grüebler *et al.*, 2010; von Post *et al.*, 2012).

Because farmsteads provide a large proportion of non-crop habitats in intensive agricultural ecosystems it is important to establish if they are sources of biodiversity and if uses of the surrounding agricultural land influence diversity in them. Furthermore, subsidies amounting to millions of Euros are paid to farmers to apply wildlife and environmentally friendly farming practices, but often we still do not know if they target optimal areas to improve biodiversity. Effects of an AES on biodiversity can only be evaluated by measuring diversity before and after its implementation. However, knowledge of the kinds of schemes that target biologically diverse farmland habitats is needed so policymakers, farmers and conservationists can evaluate national and international farmland development programs.

A further important factor to consider is that farmland landscapes have lost heterogeneity at multiple spatial scales (Benton *et al*., 2003), and restoring or increasing their heterogeneity by increasing semi-natural land use is likely to lead to increased biodiversity (Tscharntke *et al.*, 2005). However, in the main production regions this may not be politically or economically feasible. Increasing the heterogeneity of crop cover could be an alternative way to increase habitat heterogeneity with relatively low impact on production (Fahrig *et al.*, 2011), but it is still unknown if crop heterogeneity at larger spatial scales is positively related to biodiversity. Furthermore, biodiversity in farmland landscapes may be more strongly related to non-crop habitats than crop habitats. Previous studies of heterogeneity have found that species diversity increases when more habitats are sampled locally (Piha *et al.*, 2007; Billeter *et al.*, 2008; Haslem & Bennett, 2008; Pickett & Siriwardena, 2011). However, knowledge is scarce on the importance of habitat heterogeneity around specific habitats (e.g. non-crop habitats offering nest sites for farmland birds foraging in fields) in the surrounding landscape.

The Common Agricultural Policy (CAP) of the EU and national farmland development programs are revised regularly and should consider regional patterns in agriculture and biodiversity if a successful balance between production and conservation is to be reached. In addition, there is current interest in increasing biodiversity in open farmland plains of Sweden (Swedish Board of Agriculture, 2013) and Swedish environmental goals include maintenance of biologically diverse agricultural landscapes. Therefore, addressing the knowledge gaps and questions above is important for evaluating current conservation and farmland development programs, and planning future programs, in both Sweden and elsewhere.

2 Aims

The aims of the studies underlying this thesis were to obtain information that can facilitate identification of target habitats for conservation efforts in ecosystems dominated by arable land in Sweden, and assess deviations (if any) of the ecosystems' biodiversity patterns from those found in other parts of Europe. More specific objectives were to explore relationships between the following factors and both bird abundance and diversity in open agricultural landscapes:

1. Crop sowing time (Papers I–IV & Paper V[1]) and crop-specific temporal patterns in the density of field-nesting species, especially skylarks, during the breeding season (Paper I & Paper V).
2. Low intensity agricultural land use types such as leys, set-aside and pasture (Papers I–IV & Paper V).
3. Non-crop habitats such as farmsteads, infield non-crop islands, semi-natural pastures and field margins (Papers II–IV & Paper V).
4. Animal husbandry, contrasting for instance farmsteads with and without farm animals (Papers II).
5. Landscape heterogeneity and land use patterns at a 25 km^2 scale (Papers II–IV).
6. AES subsidies for specific land uses, such as organic farming, semi-natural pastures, leys and management of habitat elements with nature and cultural values (Paper III).

---

1. Paper V in preparation: Hiron, M., Berg, Å. & Pärt, T. (2014). Relationships between agricultural land use and farmland birds depend on species, species group and time in the breeding season.

3 Methods

3.1 Swedish agriculture & the study system

Farmland covers 10% of Sweden's land area, and Swedish agricultural landscapes are sometimes divided into three types: open plains[2], mosaic landscapes (large areas of farmland interspersed with woodland) and small-scale farms in forested landscapes (Wretenberg *et al.*, 2007). Some areas of arable plains in southern Sweden consist almost entirely of arable fields, covering up to 96% of the area, with scattered farmsteads and roads covering the rest. Ley is the most common agricultural land use at the national level, but cereals dominate in the productive plain regions (Jansson, 2011). The landscapes included in the studies were arable plains or farmland-forest mosaic landscapes (with large areas of contiguous arable farmland) located in the three most productive agricultural regions: Skåne, Götaland and Svealand (Fig. 4).

According to data compiled for 2009, agricultural land in these landscapes is predominantly used to produce arable crops (mean coverage, 94%) and approximately 48% of the arable land is used for cereal crops, 22% for grass, 7% is set-aside and the remaining area supports various broadleaved crops (e.g. rape, sugar beet and legumes). Autumn-sown wheat is the most widespread cereal crop, followed by spring-sown barley and oats, which accounted for 44%, 28% and 14% of the total cereal area, respectively, in the study regions in 2009.

2. The use and understanding of the term "farmland or agricultural plain" may not be the same for a person living in North- or South America and a person from Scandinavia. However, the Swedish term "slättbyggd" meaning plain is used both officially and colloquially to describe areas with large continuous areas of often arable dominated farmland.

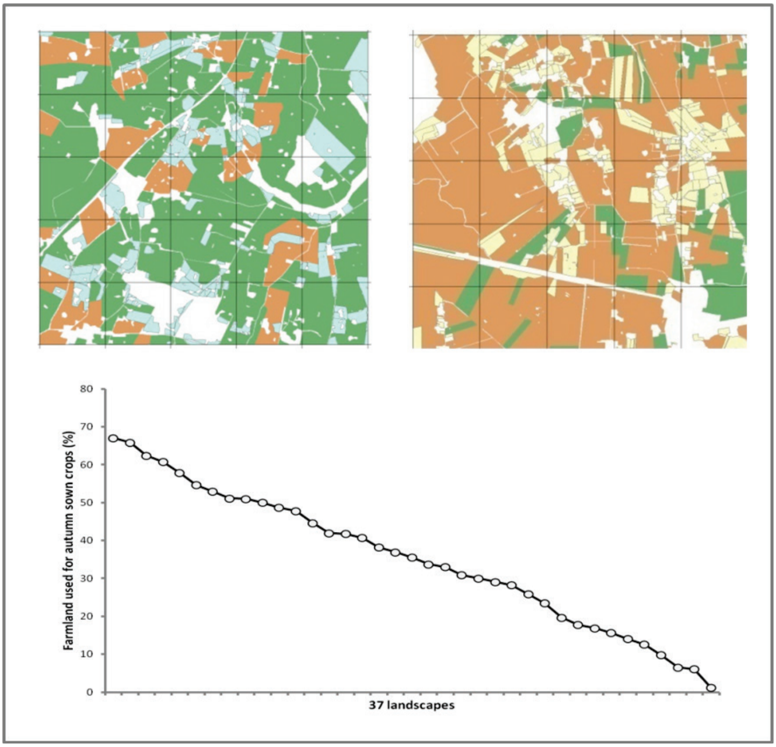

Figure 3. Graph showing the crop sow-time gradient and GIS grid squares showing two of the 37 landscapes (25 km^2) at the extreme ends of the gradient, dominated by autumn-sown crops (green) and spring-sown crops (brown).

3.2 Landscape selection

This study was designed to select count sites covering as full gradients in habitat quality as possible, at both local scale (i.e. in the proximity of the sites) and a larger landscape scale (5 km × 5 km). The latter was chosen as a landscape scale because it corresponds both to Swedish property map squares (thus facilitating summarisation of geographical data into spatial units) and roughly to the area that individual birds might move within pre- and post-breeding dispersal, and for some species during winter (Pickett & Siriwardena, 2011). The coverage of autumn-sown crops is reportedly negatively correlated to bird diversity in agricultural landscapes (Eggers *et al.*, 2011) and semi-natural pastures are generally considered important biologically diverse habitats in farmland. Therefore, correlations between these agricultural land uses and both the abundance and species richness of farmland birds were anticipated, at either local scale (i.e. a few hundred meters around transects and point count sites) or a larger landscape scale (25 km^2). Accordingly, the selected farmland landscapes covered gradients in both of these land uses.

A number of potential landscapes that met the selection criteria were chosen using data from the Swedish Board of Agriculture's GIS layer and database of agricultural land use during 2006. In further planning, 40 of these landscapes were selected for detailed consideration (aiming to minimise regional correlations in land use, e.g. in the proportion of autumn-sown crops) and 37 were subsequently used for bird surveys (Figs. 3 & 4).

3.3 Land use survey

Before establishing bird survey sites within landscapes it was essential to ensure that the agricultural land use cover was similar in 2009 to that in 2006 (the year when the data used to choose landscapes were collected), and identify where specific crops were being grown to cover variations in current local land use in and around count sites appropriately. Therefore, the land use in landscapes was mapped during field visits between January and April 2009. Fields were assigned to the following five broad land use classes that could be seen and distinguished from a distance: (1) autumn-sown crops (cereal or broad-leaved), (2) spring-sown crops (bare ground or stubble during winter), (3) cultivated grass with no signs of use for pasture, (4) pasture (divided into open bush/tree-free or with scattered trees and bushes), and (5) set-aside (land taken out of production and often non-rotational). Furthermore, structural habitats known to be important for birds (e.g. stone piles, thorny bushes and junipers in non-crop islands and pastures) were also mapped. All information was digitalised in GIS and used for further planning.

3.4 Site selection

One of the main aims was to investigate habitat-specific bird abundance and species richness and relations of these variables to agricultural land use during the year of the bird survey, both within the vicinity of the count sites and at a larger landscape scale. Some bird species only use fields if they are close to suitable nesting structures, while others avoid tall vertical structures because of the associated increases in predation risks. Therefore, we surveyed birds in three common non-crop habitats (farmsteads, n = 438; infield non-crop islands, n = 155; and bush-rich semi-natural pastures, n = 74). We also counted birds in fields of the most common crop types (autumn-sown or spring-sown crops, n =

338; leys, n = 75; set-asides, n = 25; and cultivated pastures, n = 30), but selected fields away from vertical structures (see below). We used two methods for surveying the two bird communities: strip transect surveys for species that both nest and forage in fields, and point counts for species that are associated with non-crop habitats but require open areas (such as agricultural fields) for foraging.

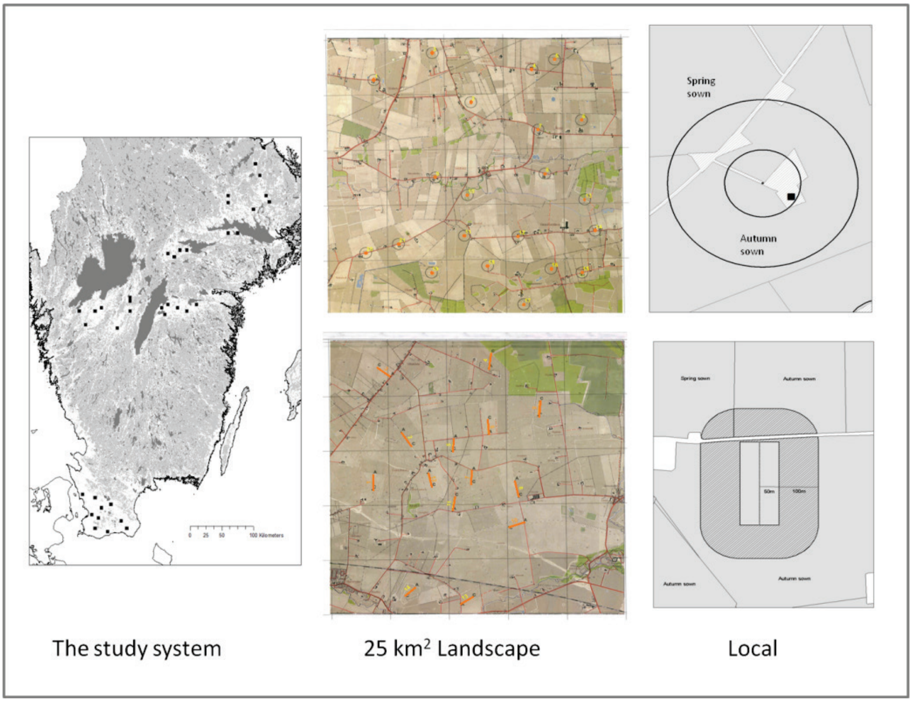

Figure 4. An overview of the study system displaying, from left to right: a map showing locations of all 37 of the selected 25 km^2 landscapes in the agricultural regions of Skåne, Götaland and Svealand (Mälaren basin); field maps showing point and transect locations; and schematic diagrams of a point count site located by a farmstead and a strip transect in an autumn-sown arable field. The circles around the point count site correspond to a 100 m radius where birds were counted within or outside the boundary, and 250 m radius, within which land use at the local scale was summarised for analyses.

3.4.1 Transects

Transects were placed either within fields or along field margins between two neighbouring fields of the same land use type (see section 3.4). Field margins with many trees and bushes were avoided to reduce negative effects of predator lookouts on the local abundance of field-nesting birds. Transects (median length = 250 m, min = 150 m, max = 300 m) were located at least 300 m apart within landscape plots to avoid doubly counting individual birds, and at least 100 m from houses, woodlands and busy roads to minimise effects of predator avoidance and human disturbance on habitat selection (Berg & Pärt, 1994; Erdos *et al.*, 2009).

3.4.2 Points

Farmsteads were chosen using aerial photographs, digital maps and information obtained from our land use survey (see above), aiming to balance the number of farmsteads with and without animal husbandry, and vary the areas covered by autumn-sown and spring-sown crops around survey points within each landscape plot. Farmstead points were placed at least 100 m from woodland or main roads to avoid these habitat structures influencing bird abundance. The point centres were placed as close to the respective farmsteads as possible. Points located in semi-natural pastures and by infield non-crop islands were also chosen (using aerial photographs, digital maps and information from our land use survey) that were located at least 100 m from farm buildings and woodland areas. Most (80%) of pastures were not classed as arable in Swedish land cover maps (i.e. with no recent history of use as croplands). These pastures are semi-natural and contain scattered trees and bushes and boulders (ranging from large blocks to small rock piles). Infield non-crop islands are situated within arable fields and are small, uncultivated patches of rocks, stone piles or old mudstone pits, often with shrubs and trees.

3.5 Statistics

Poisson or binomial Generalised Linear Mixed Models (GLMMs) were used in Studies I, II, III and V (Figs. 7–9) to analyse count data and species presence-absence data with nested random effects to account for spatial dependence of data points (count sites in landscapes). For true Poisson distributions the mean equals the variance. However, field data often do not meet this criterion because they are over-dispersed. Thus, when data were considered over-dispersed, observation level random effects were added to the models to reduce parameter estimate bias (see Zuur *et al.*, 2012 for a recent description).

No hypothesis testing or stepwise model selection procedures were applied in any studies summarised in this thesis since important information may be lost if variables are dropped because a selected significance criterion is not met (e.g. $P < 0.05$). Furthermore, assumptions that the final model left after applying stepwise procedures is the only plausible model may be wrong. In many cases (especially when modelling noisy ecological data) a number of equally likely or nearly as likely models could be the best. This model selection uncertainty is ignored in stepwise selection and may bias parameter estimates (Whittingham *et al.*, 2006). Multi-model inference (Burnham & Anderson, 2010) can be used to minimise some of these statistical issues. The metrics calculated from multi-model inference (relative variable importance, ΔAIC, model weights etc.) and adjusted parameter estimates give more comprehensive indications of explanatory variables that are definitely important, probably important, potentially important and probably unimportant. Furthermore, they allow insight and evaluation of the strength of evidence for all models that could plausibly explain the observed data.

Figures 7, 8 and 9 show results (to be presented in Paper V, in preparation & not included in the thesis) of analyses of data from the transect survey and point counts using the basic mixed model structures described in Papers I and II, respectively, but with different response and explanatory variables.

4 Results and discussion

4.1 Bird communities in fields and non-crop habitat patches

Skylark was the most common bird species in transects in fields (Fig. 5a), which is not surprising because this part of the study was designed to investigate species nesting in fields. The next most frequently observed field-nesting species were lapwing, meadow pipit (*Anthus pratensis*) and yellow wagtail (*Motacilla flava flava*), although the latter species was observed in fewer than 10% of transects. Other commonly observed species in field transects were jackdaw (*Corvus monedula*), hooded crow (*Corvus corone cornix*) and starling. The four most common species counted at farmstead point count sites were tree sparrow (*Passer montanus*), jackdaw, starling and white wagtail (*Motacilla alba alba*) (Fig. 5b). In contrast, yellowhammer (*Emberiza citrinella*), whitethroat (*Sylvia communis*), wheatear (*Oenanthe oenanthe*), linnet (*Carduelis cannabina*) and whinchat (*Saxicola rubetra*) were observed more often in semi-natural pastures and/or infield islands than at farmstead sites.

4.2 Effects of crop sowing time: spring- vs. autumn-sown crops

Crop type and crop structure influence birds' habitat choice (Chamberlain *et al.*, 1999; Wilson *et al.*, 2005; Gilroy *et al.*, 2010; Eggers *et al.*, 2011), reproductive output and survival (Chamberlain & Crick, 1999). Some species have been shown to switch crops as field layer vegetation becomes tall and dense during the breeding season (Gilroy *et al.*, 2010; Eggers *et al.*, 2011). Autumn-sown crops and spring-sown crops form extremes of a vegetation height gradient in arable fields, especially in spring and early summer (Fig. 6).

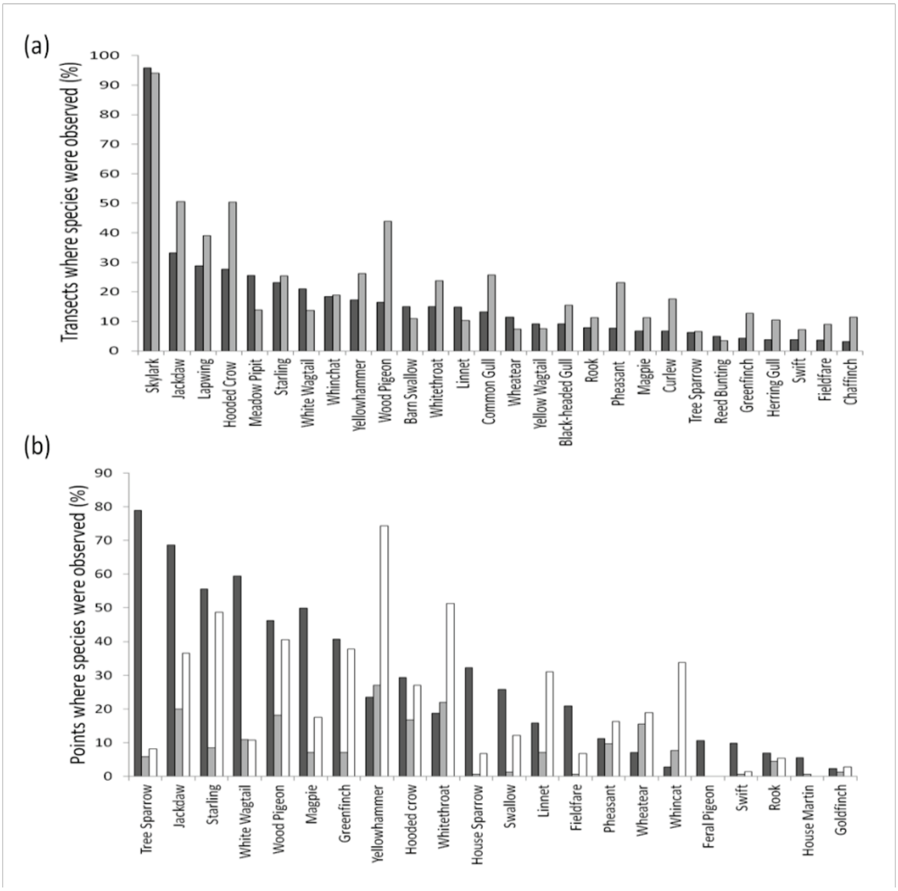

Figure 5. Percentages of count sites where species were observed. Panel (a) shows pooled data from the surveys of strip transects in five crop types. Dark grey bars indicate observations within the strips 50 m either side of the transect line and light grey bars observations outside of the strips (unlimited distance), n = 527. Panel (b) shows data from the point count survey (non-crop nesting species only) at farmsteads (dark grey), n = 437; infield non-crop islands (light grey), n = 155; and semi-natural pastures (white), n = 74. The point counts only include species recorded on at least two occasions at a site (see Paper II, Methods), but the transect data include all observations (single and multiple) during the season.

The switch from spring-sown to autumn-sown crops (especially cereals) during modernisation of farming is regarded as an important contributor to farmland bird declines in some parts of Europe (Newton, 2004; Butler *et al.*, 2007; Donald, 2004).

4.2.1 Skylark — a seasonal shift in land use preference

A strong relationship between sowing time, time in the breeding season and abundance was found for the skylark (Fig. 12c & Paper I), a farmland species that both nests and forages in crop fields. Seasonal declines in skylark abundance in tall autumn-sown crops during the breeding period and contrasting stable (or increasing) abundance in shorter spring-sown crops have also been documented in other studies (Chamberlain *et al*., 1999).

Figure 6. Spring-sown (left) and autumn-sown (right) cereal crops in early June in Svealand, illustrating differences in habitat structure for ground foraging/nesting birds during the period when they feed their nestlings. Photo: Sönke Eggers.

However, our study shows that skylarks clearly prefer autumn-sown crops over spring-sown crops early in the breeding season in the study region. Higher skylark abundance in autumn-sown crops early in the breeding season has also been found in agricultural landscapes of south-central Sweden and Finland (Piha *et al*., 2003; Eggers *et al*., 2011). In contrast, skylarks reportedly have higher abundances in spring-sown cereals throughout the season in lowland farmland in the UK (Donald, 2004), or no difference that depends on sowing time early in the season followed by declines in autumn-sown cereals (Chamberlain *et al*., 1999). The reason for these differences may be that the ground is bare in spring-sown fields in Sweden when many skylark territories are established (late April and early May). Thus, as skylarks require some vegetation for nest concealment (Donald, 2004), fields with autumn-sown crops that are around 10 or 12 cm high and have sparse ground cover probably provide more suitable nesting habitat than spring-sown fields with no vegetation cover.

The relative quality of habitats provided by autumn-sown and spring-sown crops may also vary with time. Our data show that skylark numbers halved in fields with autumn-sown cereals over the breeding season, indicating that habitat quality in them declined markedly, possibly as the crops became tall and dense. In contrast, numbers were stable in spring-sown cereals (but low at the beginning of the breeding season). These patterns could be indications of an "ecological trap" (Battin, 2004) where birds may potentially choose relatively poor habitats because of differences in vegetation height at the beginning of the breeding season. On the other hand, birds that nest early (e.g. in autumn-sown crops) may have higher fitness than later breeders (e.g. in late growing spring crops) (Öberg *et al., 2013*), Thus, demographic data are needed for a more detailed evaluation of the habitat quality of spring-sown and autumn-sown crops in Swedish farmland (see discussion in Paper I).

Skylarks were observed at 97% of the approx. 500 field transects surveyed (Fig. 5a.), indicating that this species is still very widespread in intensive agricultural regions. One reason why skylarks are still very widespread and common in Sweden could be that even in the most intensive farmland landscapes there is still a mixture of autumn- and spring-sown crops, so at a landscape scale short vegetation is available throughout the breeding season. This suggests that ecological perturbations caused by the switch to autumn-sown crops that have caused strong concern in the UK may be much less important for farmland bird populations in many agricultural areas of Sweden. It also has implications for conservation measures. A popular practice of creating so-called skylark patches in arable fields has been adopted in the UK (Morris *et al.*, 2004) and Sweden (Sveriges Ornitologiska Förening, 2013). However, given the coverage of spring-sown crops (with relatively short vegetation) in many farmland areas in Sweden, creating small unsown patches in autumn-sown crops may not substantially benefit skylark populations in all Swedish agricultural landscapes. Results presented in Papers I and IV show that skylark abundance is higher in autumn-sown cereals, the species' abundance is not significantly related to areas of spring-sown crops surrounding autumn-sown crops and the proportional cover of autumn-sown crops at a landscape scale is not related to the diversity of field-nesting bird species (of which skylark is a main component). Thus, further research is required on the effectiveness of skylark patches (and alternative measures) in different regions (see also Berg & Kvarnbäck, 2011).

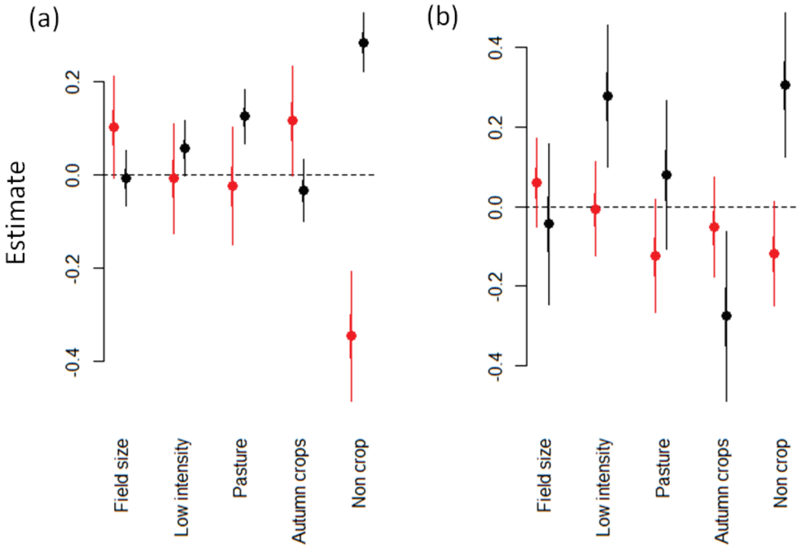

Figure 7. Results from GLMMs using point count data to investigate effects of different land uses on the abundance of field-nesting birds (red) and non-crop nesters (black) at farmsteads (a) and in non-crop islands (b). Land uses refer to proportional coverage within a 250 m radius around point count centres except for non-crop, which refers to coverage within a 100 m radius (the area where birds were counted).

4.2.2 Other farmland bird species

Other field-nesting species are also likely to be affected by the time when crop fields are sown. For example, lapwings have been previously shown to avoid autumn-sown crops during the breeding season (Berg *et al.*, 1992; Kragten & de Snoo, 2008) and yellow wagtails switch from autumn- to spring-sown fields during the breeding season (Gilroy *et al.*, 2010) in a similar manner to Swedish skylarks. However, many bird species nesting in non-crop habitats in farmland are ground foragers and also use crop fields to find food. Therefore, the contrast in vegetation height between autumn- and spring-sown crops could affect habitat quality in terms of food availability, and hence the abundance of ground-foraging species and their species richness as a group (Anderson *et al.*, 2001). Thus, possible effects of the proportional cover of autumn-sown crops in the local landscape around farmsteads (a major nesting habitat in farmland plains) on the abundance and species richness of birds in this habitat were investigated in further studies (Paper II). No effect of this variable on non-crop nesting birds was detected, indicating that the coverage of autumn-sown crops around farmsteads does not significantly affect numbers of either individuals or species in them. In contrast, preliminary results (Paper V in preparation) of surveys of in-field non-crop islands suggest that the proportion of autumn-sown crops in the vicinity is negatively related to the abundance of non-crop nesting birds (Paper V, Fig. 7), as previously shown in Swedish farmland (Eggers et al., 2011). One reason for this contrast between farmsteads and infield islands could be that more resources are available at farmsteads, whereas birds nesting in infield non-crop islands might be more dependent on resources in surrounding arable fields (discussed in Paper II, see also Paper III) and more strongly affected by field layer vegetation height (see Low *et al.*, 2010). However, at the 25 km^2 landscape scale we found no relationship between the proportional cover of autumn crops and species richness (Paper IV).

4.3 Effects of low intensity arable land uses – cultivated grasslands and set-asides

Disturbance frequently occurs in annual crop fields during the year. Some fields that could be used for annual crop production are used as cultivated pastures, leys or permanent set-asides, which are managed less frequently, receive less chemical inputs than annual crops and remain under the same management regime for several years. The absence of annual disturbance (e.g. tillage and pesticide applications) may allow weeds to establish and promote a varied vegetation structure (Henderson *et al.*, 2000), which could increase resource availability for farmland birds (Marshall *et al.*, 2003; Wilson *et al.*, 2005). In addition, the presence of grazing animals in cultivated pastures may increase invertebrate availability through grazing, trampling and dung production (Buckingham & Peach, 2005).

Results from the transect surveys showed that densities of birds were generally higher in low intensity fields than in annual crop fields (Paper V, Fig. 8). This difference was particularly notable for non-crop nesting bird species, which were likely to be mainly foraging individuals since transects were chosen to avoid vertical structures. Furthermore, the density of non-crop nesters increased during the breeding season in low intensity fields (especially cultivated pastures, but also leys), suggesting that suitable food items are more available in them than in annual crop fields. Although cultivated leys and pastures are less intensively managed than annual crop fields, these grasslands are managed more intensively than their semi-natural counterparts.

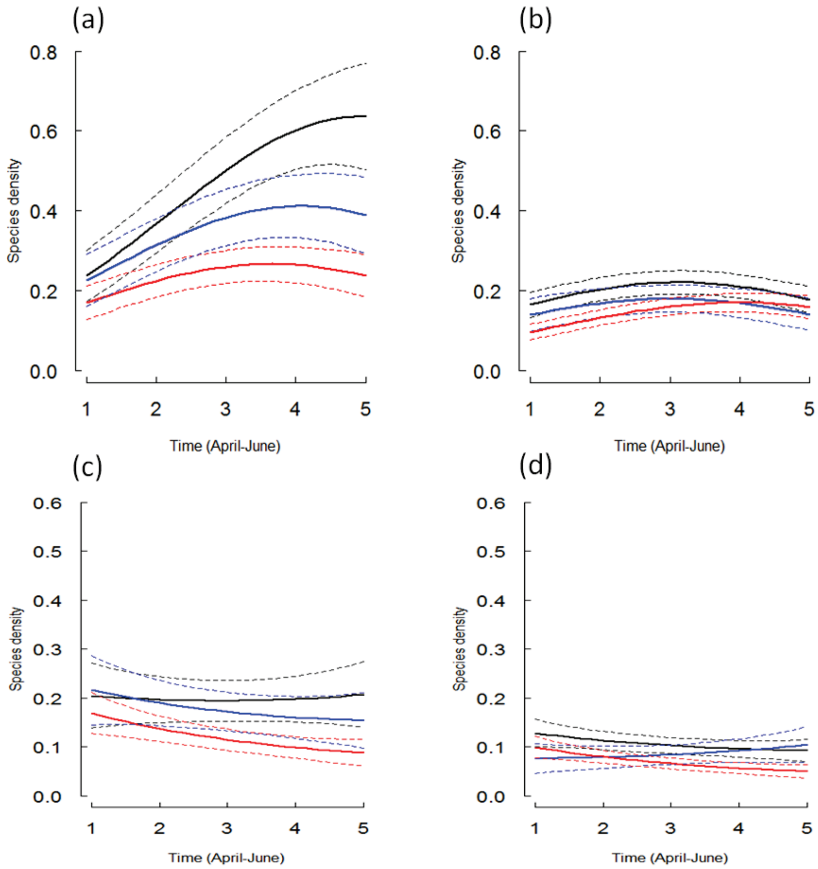

Figure 8. Results from GLMM analysis of strip transect data to investigate the effects of different land uses on temporal trends of non-crop nesting species (a-b) and field-nesting species (excluding skylark as these results are presented in Paper I) (c-d). Panels a & c: black = cultivated pasture, blue = set-aside, red = ley. Panels b & d: black = spring cereals, red = autumn cereals, blue non-cereal spring crops

Morris et al. (2001) found that modern intensive grasslands are poor foraging habitats for yellowhammers. However, it has been shown that low intensity arable land (e.g. cultivated pastures and set-asides) may benefit birds if they are otherwise rare in the landscape (Wretenberg *et al.*, 2010). This "rare habitat effect" may also occur in arable crop fields in grassland-dominated areas in the UK (Robinson *et al.*, 2001). The increase in land use heterogeneity caused by the presence of both crop and grass fields could result in habitat complementation, leading (for instance) to the availability of various seed and invertebrate resources at different times throughout the year, thus benefitting species with multiple habitat requirements.

4.4 Effects of non-crop habitats and habitat elements

Another potentially important aspect of agricultural intensification is the loss of non-crop habitat elements, such as stone walls, surface ditches and infield non-crop islands, to allow for more efficient farming practices (Robertson *et al.*, 1990; Ihse, 1995). Although the studies in this thesis were primarily designed to investigate effects of land use in surrounding fields on habitat-specific abundance and species richness of birds (i.e. birds in open fields, farmsteads, infield non-crop islands and semi-natural pastures), the most constant predictors of bird diversity were measures of non-crop habitat elements within the local landscapes (Papers II, IV and V, Figs. 7 & 9).

The abundance and species richness of both field-nesting bird species and species nesting in non-crop habitats were higher in transects along open ditches than those within fields or along grass margins (Paper V, Fig. 9). Previous studies have shown the value of open drainage ditches (reviewed by Herzon & Helenius, 2008) that potentially provide open areas with damp ground where vegetation-gleaning and soil-probing species can forage. In many farming landscapes surface drainage ditches have been replaced by subsoil drains when field sizes have been increased to facilitate more effective farming (Jansson, 2011). In addition, the species richness of non-crop nesters was higher in all types of margins than in the middle of crop fields (Fig. 9b), clearly suggesting that removing boundaries (e.g. to create larger fields) negatively affects biodiversity in field ecosystems. Bird abundance and (probably) species richness were also higher in fields with AESs for nature-cultural elements (e.g. old buildings, non-crop islands, open ditches, old tracks and stone walls) than in fields lacking subsidies for these elements (Paper III).

Clearly these relationships are partly attributable to non-crop nesting species' needs for non-crop habitat elements for nesting (Fig. 7). This is consistent with a conclusion in Paper IV that the species richness patterns in this bird group are influenced by the local abundance of non-crop habitats, but not landscape-scale cropping patterns. Other studies have also shown that non-crop elements enhance bird diversity in farmland (e.g. Berg, 2002; Fuller *et al.*, 2004; Herzon & O'Hara, 2007; Billeter *et al.*, 2008).

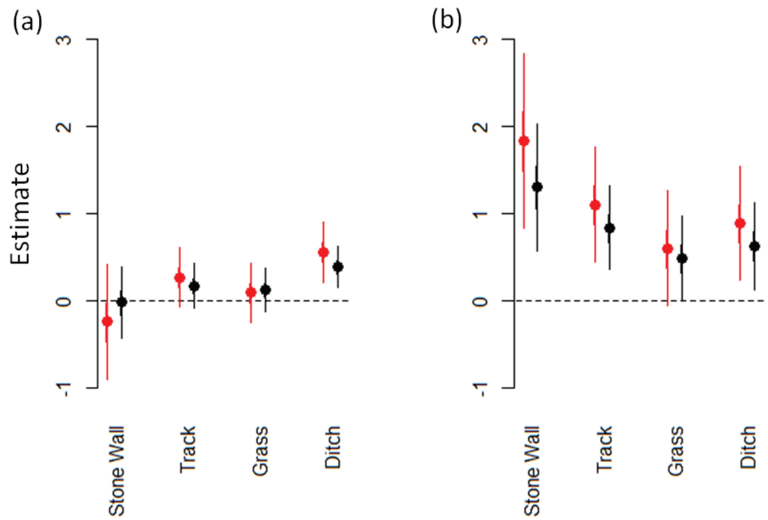

Figure 9. Results from GLMMs using data from strip transects in spring-sown fields to investigate effects of field margins on the abundance (red) and species richness (black) of field-nesting species (a) and non-crop nesting species (b). Margin effects were evaluated by comparing differences in data obtained from transects in margins and the base line category "infield", i.e. transects situated in the middle of crop fields.

However, it is important to remember that many field-nesting species might be negatively affected by non-crop landscape elements, especially vertical structures that might be used as predator lookouts (Berg & Pärt, 1994; Suhonen *et al.*, 1994). Analyses of observations of field-nesting species at non-crop point count sites showed a negative relationship between bird abundance and the proportional cover of non-crop habitat at the local level (Fig. 7). The same pattern was also observed at the landscape scale, as the total number of field-nesting species was found to be lower in landscapes consisting of larger areas of non-crop habitats than in more homogeneous agricultural landscapes (Paper IV). Undoubtedly, the effects of changes in the proportional cover and distribution of non-crop habitats and habitat elements on the farmland bird community will differ markedly depending on the breeding ecology of species.

Figure 10. A simplified farmland landscape in southern Sweden showing the distribution of farmsteads (potentially important bird habitat) in a landscape dominated by arable fields.

4.4.1 Farmsteads as hotspots for non-crop nesting bird species

In the productive agricultural plain regions of Sweden farmsteads are sometimes the main non-crop habitats in a sea of arable fields, as illustrated in figure 10. Farmsteads include habitat elements such as deciduous trees, bushes, gardens, barns and other buildings, farmyards and (if animals are present) paddocks and manure heaps, all of which can be used by birds (Barnard, 1980; Ambrosini *et al.*, 2002; Fuller *et al.*, 2004; Ahnström *et al.*, 2008; Grüebler *et al.*, 2010).

However, a key issue is whether farmland birds are abundant in farmsteads in intensive and highly simplified farmland during the breeding season, or they are largely unoccupied because of a lack of food resources in the surrounding landscape. Results presented in Paper II show that farmsteads are not only species-rich in comparison to semi-natural pastures and infield non-crop islands, but also that the density of individual birds and their species richness increase in farmsteads as landscapes become more intensive (with larger fields). This suggests that farmland birds become more concentrated in farmsteads as landscapes become more simplified (see also Fig. 12b). Thus, increasing the amount of available resources (nest sites and food availability) in and around farmsteads could enhance biodiversity even in the most intensive farmland.

Major changes in Swedish agriculture over the last four decades have included reductions in numbers of farm holdings in general and farm holdings with animals in particular (see section 4.5). Results presented in Paper II also show that the species richness and abundance of birds were lowest in inactive farmsteads (presumably now only used as homes for people), intermediate in farmsteads that are still used for agricultural production and highest in farmsteads with animal husbandry (see discussion below).

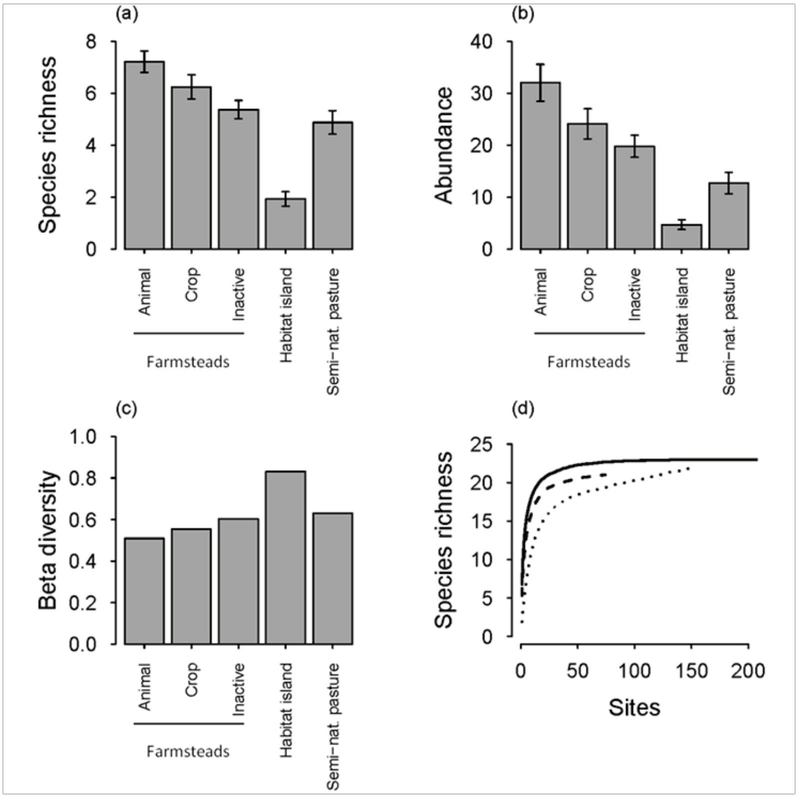

Figure 11. Observed species richness (a), abundance (b) and beta diversity (c) of 22 farmland bird species at points of five categories: farmsteads with animals (n = 140), farmsteads where only crops are produced (n = 107), farmsteads (old farms) with no current active farming (n = 169), infield non-crop islands (n = 155), and semi-natural pastures (n = 74). Error bars are 95% confidence intervals. Abundance is expressed as the maximum number of individuals counted at each site during five survey visits, and beta diversity as an average measure of dissimilarity (Sorensen's index) at each site category, with values ranging from zero for complete similarity (i.e. all sites within each category sharing the same species) to one for complete dissimilarity (no shared species). Panel d shows species accumulation curves for farmstead sites pooled (solid line), semi-natural pastures (dashed line) and infield non-crop islands (dotted line). The figure is used with permission of the publisher.

4.5 Effects of animal husbandry and pastures

The loss of mixed farming (i.e. both animal and crop production) at multiple scales from farms and landscapes to regions has been implicated as a contributor to farmland biodiversity declines (Pain & Pienkowski, 1997; Robinson *et al.*, 2001; Benton *et al.*, 2003). In some agricultural areas of Sweden, nearly 80% of farm holdings with cattle have been lost since 1970 (Fig. 2). The decline in the number of cattle has been less acute, indicating that average numbers of cattle on the remaining active farms have increased, probably due to increasing specialisation in either crop or animal production.

Local species richness and abundance of birds were higher on farmsteads (i.e. at the farms) with animals than on both farmsteads where only crops were produced and former farmsteads where there was no active farming. The main agricultural land use surrounding farmsteads that related to bird diversity was pasture, again suggesting that animal husbandry is important for the diversity of non-crop breeding farmland birds. The availability of safe nest sites at farmsteads and resource-rich foraging grounds (e.g. pastures, paddocks and manure heaps) in close proximity is probably very beneficial to farmland bird species nesting in intensive farmland (Bruun & Smith, 2003; Evans *et al.*, 2007). The presence of farm animals in farmsteads or pastures in the local landscape was clearly beneficial for the abundance of starlings, house sparrows, swallows, and house martins (and potentially beneficial for a larger number of species, according to model parameter estimates).

Semi-natural pastures have previously been shown to be important bird habitats in farmland (Pärt & Söderström, 1999; Söderström & Pärt, 2000; Vickery *et al.*, 2001; Virkkala *et al.*, 2004). Results presented in Paper III also show that local species richness increased when the proportional cover of semi-natural pastures subsidised by agri-environment payments increased in the neighbourhood. Similarly, the abundance and species richness of farmland birds was positively correlated with low intensity land uses such as leys, cultivated pastures and set-asides (see section 4.3, Fig. 8), of which ley and cultivated pastures are of course connected to animal husbandry. Thus, many important bird habitats in farmland are both historically and currently associated with animal production, emphasising that the decrease in animal husbandry should be viewed as a serious threat to biodiversity in agricultural ecosystems.

4.6 Agri-environment schemes

An important issue is the degree (if any) that AESs target the most important habitats (see e.g. Kleijn *et al.,* 2011). This was addressed by modelling relationships between agri-environment payments and the local abundance and species richness of farmland birds (Paper III). The data used were point counts (in farmsteads, non-crop islands and semi-natural pastures), the areas of subsidised land uses in the surrounding landscape and other land use variables. The results showed that the coverage of subsidised leys (with and without signs of use as pastures) correlated with the abundance and species richness of birds. Non-subsidised pastures had higher abundance of birds, but not species richness, while the proportional cover of subsidised semi-natural pastures positively correlated with both species richness and abundance (see discussion in Paper III). In addition, land covered by AES for maintenance of elements with nature-cultural values positively related to the abundance of farmland birds, providing further evidence that non-crop habitat elements (e.g. old buildings, open ditches, stone walls, and non-crop islands) are important for some bird species in farmland.

Organic farming is a land use that is eligible for agri-environment subsidies, at either the farm or field level. It could potentially increase bird diversity because of the associated reductions in chemical inputs, which can increase resource availability for farmland birds by increasing seed and insect abundance and reducing the density of crop swards (Hole *et al.*, 2005). However, many organic farms are located in landscapes with relatively high levels of non-crop elements and/or mixed (crop and animal) farming (Hole *et al.*, 2005; Gabriel *et al.*, 2009; Norton *et al.*, 2009). This can complicate attempts to disentangle effects of organically managing arable fields from those of variations in landscape structure and other farming practices. However, the confounding effects of landscape structure (see also Paper IV) and organic farming were minimized by focusing on farmland plain regions and counting birds in specific non-crop habitats within them.

No positive relationship was detected between areas of organic farming within 250 m of specific habitats on bird diversity and abundance. This suggests that although organic farming could provide more resources for farmland birds in homogenous farmland (Smith *et al.*, 2010) it did not lead to higher bird numbers or species richness in the specific habitats surveyed. However, species richness increased as the area of organic fields increased at the 25 km^2 landscape scale, suggesting that high uptake of this AES had a positive effect at the landscape level (for discussion of AES and uptake scale see also Dallimer *et al.*, 2010; Gabriel *et al.*, 2010; Whittingham, 2011), but only in the most extreme agricultural landscapes consisting almost entirely (> 90% cover) of arable fields.

4.7 Alpha, beta and gamma diversity of farmland birds

Habitat-specific conservation strategies need to take into account the distribution of diversity between the local (alpha), between-site (beta) and regional (gamma) spatial scales. This is because in order to enhance biodiversity it is better to focus conservation efforts on a few farmland habitat patches with relatively high alpha diversity when there is a general pattern of high alpha and low beta diversity (i.e. relatively high species richness and low variation in species richness between sites). However, if there is a general pattern of low alpha and high beta diversity (i.e. relatively low species richness and high variation in species richness between sites) it is better to protect many local patches. Both infield non-crop islands and semi-natural pastures had higher beta diversity (due to low alpha diversity and relatively high gamma diversity) than farmsteads in the study region. Thus, sufficient small semi-natural pastures and infield non-crop islands should be maintained in arable dominated landscapes to enhance total diversity at a larger scale.

Clearly, many farmland habitat types have high beta diversity. Therefore, an important diversity component in agro-ecosystems is ignored if only alpha diversity at a local patch scale is considered when investigating effects of landscape land use patterns on species richness (Clough *et al.*, 2007; Hendrickx *et al.*, 2007; Gabriel *et al.*, 2010). Results presented in Paper IV showed that species richness observed at a local scale (i.e. alpha diversity) did not always reflect species richness patterns at a landscape scale (i.e. gamma diversity). Similar numbers of species were detected locally across land use gradients, but the species pools (gamma diversity) of field-nesting species declined as landscapes became more heterogeneous in terms of non-crop cover. This provides further support for the views that some farmland birds respond negatively to certain elements of landscape heterogeneity (Chiron *et al.*, 2010; Báldi & Batáry, 2011; Pickett & Siriwardena, 2011) and that important biodiversity patterns might be missed if only alpha diversity is considered (Clough *et al.*, 2007; Hendrickx *et al.*, 2007).

4.8 Landscape heterogeneity

Many habitats have been lost in intensive farmland, which has led to reductions in landscape heterogeneity at multiple spatial scales (Benton 2003). Increasing areas of non-crop and semi-natural habitats in farmland is likely to benefit biodiversity in all but the most heavily cleared landscapes, and landscapes where non-crop habitats are already very common (Tscharntke *et al.*, 2005). However, in many agricultural regions it will be impractical to create areas of non-productive land, especially large tracts. Therefore, it has been suggested that increasing heterogeneity in crop cover could benefit biodiversity without substantially reducing agricultural productivity (Fahrig *et al.*, 2011).

Paper IV shows that landscape-level heterogeneity of crop cover did not generally relate strongly to species richness of farmland birds at a 25 km^2 scale in the study region. However, compositional heterogeneity of crops (the coverage and evenness of different crop types) did seem to relate positively to the gamma diversity of field-nesting birds, but only in landscapes with the lowest configurational heterogeneity (i.e. the largest fields). This pattern might result from field-nesting species preferring large fields (because of predator avoidance) and requiring diverse crops for foraging. This relationship between crop cover heterogeneity components and bird diversity requires further investigation, but studies on the ecology of two field-nesting species, skylark and yellow wagtail (Wilson *et al.*, 1997; Morris & Gilroy, 2008; Donald, 2004; Gilroy *et al.*, 2010), support this conclusion.

5 Conclusions

This study was conducted during the breeding season at specific habitats when central place foraging (Orians & Pearson, 1979) partly dictates habitat selection because of the need of good foraging habitats (e.g. pastures) close to safe nest sites (e.g. deciduous trees and farm buildings for cavity nesters). When birds are not tied to their nesting habitat they are free to roam, and resource requirements may change (e.g. from predominantly invertebrate based to seed based diet). Thus, land use in annual crop fields may be highly important during the pre-, post- and non-breeding seasons for many bird species (e.g. Gillings *et al.*, 2005; Baker *et al.*, 2012). However, during the breeding season in the agricultural plains dominated by intensively managed annual crop fields, relatively small areas of non-crop habitat or fields managed with low intensity (compared to annual crops) can provide safe nest sites and accessible foraging sites for farmland birds.

Thus, land use heterogeneity at the small spatial scale of a few hectares that provides ecological contrasts (Kleijn *et al.*, 2011) in landscapes with large proportions of homogeneous, annual crop fields is vital for local bird diversity. Accordingly, I found that abundance or species richness related to crop sowing time, low intensity arable land use and semi-natural pastures at a local level. However, at the 25 km^2 landscape level the proportional cover of autumn sown crops, low intensity land uses, or semi-natural pastures was not related to local habitat-specific bird diversity, or indeed species richness patterns at larger scales. Thus, it appears that effects of agricultural land uses at larger landscape scales (across the gradient we studied) on species richness in specific habitats are small compared to those of land uses in the local environment where species' daily resource requirements are met.

Some habitat patches in farmland are characterised by high variation in species composition and low species richness, potentially because of small patch size, variable local environmental conditions and inter- and intra-specific interactions. When this beta diversity is a significant part of species richness at a landscape or regional scale (gamma diversity) it is important to recognise that many “species poor” habitats can, in their sum, maintain a large part of total biodiversity in a landscape or region. It then follows that planning and evaluation of conservation measures for farmland birds requires a “many small streams make a great river” approach – to use the Swedish proverb.

My results show that the accumulated species richness of a guild of field-nesting birds was highest in the most simplified agricultural landscapes studied. Therefore, the open agricultural plains should not be completely forgotten when evaluating and planning conservation measures for farmland biodiversity and especially not for field-nesting farmland species like skylark, lapwing, and curlew. Similarly, the farmstead is an important farmland bird habitat that should not be forgotten, especially not in the agricultural plains. This is because the density of non-crop nesting farmland birds was highest at farmsteads in more intensive farmland suggesting that farmsteads are the main places where these species can find the combination of nesting habitat and food resources in these landscapes. Furthermore, a general finding that farm animals and land uses associated with them increase bird diversity in arable crop dominated farmland suggests that incentives to maintain or increase areas with mixed farming will benefit many farmland bird species in agricultural plain regions.

Besides showing that farmland plains are not “biodiversity deserts” I show that agri-environment schemes target important bird habitats in these landscapes. Although results covered in this thesis suggest that the effects of agricultural land use on farmland birds are often strongest at the local scale, they also indicate that a landscape approach is needed when addressing conservation of farmland biodiversity. This is because effects of adjacent land use will increase beta diversity even of the same habitat type and high beta diversity is also expected between patches of different habitat types such as open fields, farmsteads, semi-natural pastures and non-crop islands. Therefore, any conservation actions aimed at farmland birds need to include many habitat patches and a landscape context.

5.1 Future challenges and questions

The breeding season is one part of the complex life cycles of birds that are dependent on many habitats over many political borders. Many birds are migratory and establishing if local conservation actions in Swedish farmland will benefit populations at larger scales will be a future challenge. However, a number of other future research questions have arisen from results and patterns found in this study. Four of these patterns are shown in figure 12 and are described below.

- From Paper IV: The positive effects of crop cover heterogeneity (Shannon index) on field-nesting birds that only starts to become apparent in the most extreme farmland plain landscapes with large fields (Fig. 12a). These results need to be scrutinized by increasing statistical power (i.e. increasing sample size of the most extreme landscapes). An interesting question is whether certain combinations of crops are better than others.
- From Paper II: The fact that species and individual density (per unit non-crop habitat) at farmsteads increases as landscapes become dominated by larger fields (Fig. 12b). Is this a concentration effect (i.e. more individuals and species at the few remaining nesting habitat patches) or are farmsteads in productive plains just top quality habitats with plentiful resources for many farmland bird species? Furthermore, does species composition change over this gradient and if so, which species types are added and removed, respectively?
- From Paper I: Are autumn-sown fields ecological traps or good habitat for skylarks (Fig. 12c) and other field nesting species? This can only be tested by collecting demographic data for these species.
- From Paper III: The contrasting effect of increased levels of organic farming that depends on landscape type (completely open plain – more forest) (Fig. 12d). Is this pattern due to different land uses being targeted for organic farming in different landscapes, or to bird community differences in species composition?

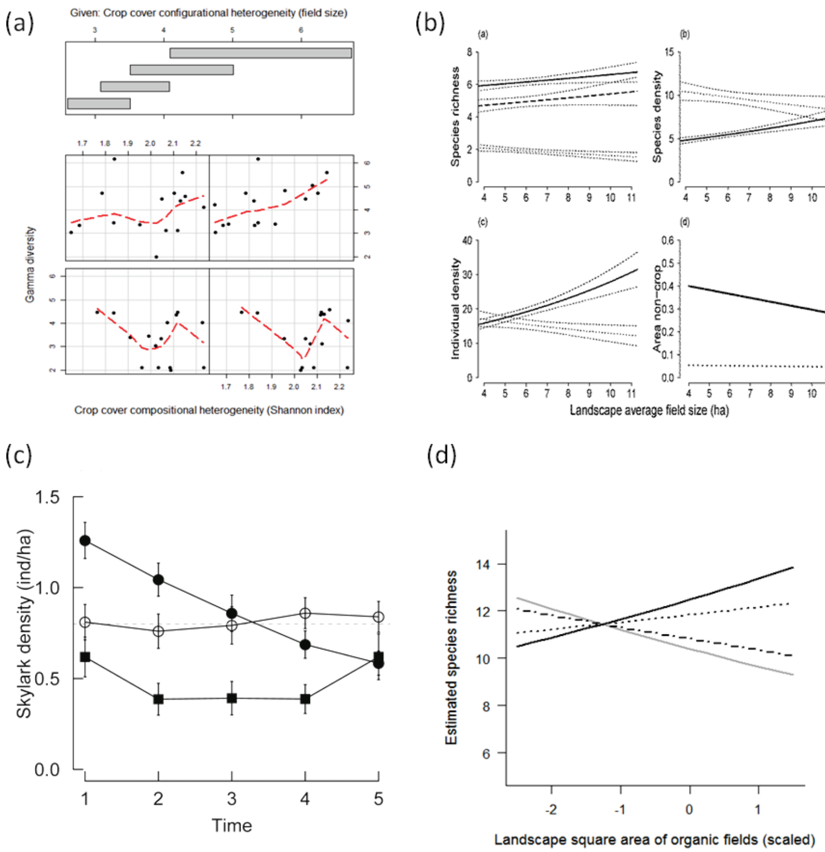

Figure 12. Patterns for further study (see above). Panel (a) is from Paper IV and shows that crop heterogeneity (measured as Shannon index) seems to relate the gamma diversity of field-nesting birds in the study landscapes with the largest average field size, (b) is from Paper II and shows that individual and species density of farmland birds at farmsteads (black lines and errors) increases as landscapes have higher average field sizes, (c) is from Paper I and shows that early in the breeding season skylarks prefer autumn-sown cereals (black circles), over spring-sown cereals (open circles) and non-cereal spring-sown crops (squares) and (d) is from Paper III and shows that increased area of organic farming at the landscape scale (25 km^2) has different relationships with species richness that depend on landscape structure – i.e. from open farmland (black) to higher coverage of woodlands (grey). Figures are used with permission of the publisher where applicable.

References

Aebischer, N. J., Green, R. E. & Evans, A. D. (2000). From science to recovery: four case studies of how research has been translated into conservation action in the UK. *Ecology and conservation of lowland farmland birds* 43–54.

Ahnström, J., Berg, Å. & Söderlund, H. (2008). Birds on farmsteads - effects of landscape and farming characteristics. *Ornis Fennica* 85, 98–108.

Ambrosini, R., Bolzern, A. M., Canova, L., Arieni, S., Møller, A. P. & Saino, N. (2002). The distribution and colony size of barn swallows in relation to agricultural land use. *Journal of Applied Ecology* 39(3), 524–534.

Anderson, G. Q. A., Bradbury, R. B., Evans, A. D. & Royal Society for the Protection of Birds (2001). *Evidence for the effects of agricultural intensification on wild bird populations in the UK*. RSPB, Sandy, UK.

Baker, D. J., Freeman, S. N., Grice, P. V. & Siriwardena, G. M. (2012). Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship scheme. *Journal of Applied Ecology* 49(4), 871–882.

Báldi, A. & Batáry, P. (2011). Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. *Ibis* 153(4), 875–876.

Barnard, C. J. (1980). Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Animal Behaviour* 28(1), 295–309.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 278(1713), 1894–1902.

Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. (2010). Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems & Environment* 136(1–2), 35–39.

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations.*Conservation Biology* 18(6), 1482–1491.

Bengtsson, J., Ahnström, J. & Weibull, A. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42(2), 261–269.

Benton, T. G., Bryant, D. M., Cole, L. & Crick, H. Q. P. (2002). Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39(4), 673–687.

Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18(4), 182–188.

Berg, Å. (2002). Composition and diversity of bird communities in Swedish farmland–forest mosaic landscapes. *Bird Study* 49(2), 153–165.

Berg, Å. & Kvarnbäck, O. (2011). Density and reproductive success of Skylarks *Alauda arvensis* on organic farms – an experiment with unsown skylark plots on autumn sown cereals. *Ornis Svecica* 21, 3-10.

Berg, Å., Lindberg, T. & Källebrink, K. G. (1992). Hatching Success of Lapwings on farmland: differences between habitats and colonies of different sizes. *Journal of Animal Ecology* 61(2), 469–476.

Berg, Å. & Pärt, T. (1994). Abundance of breeding farmland birds on arable and set-aside fields at forest edges. *Ecography* 17(2), 147–152.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J. P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M. J. M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W. K. R. E., Zobel, M. & Edwards, P. J. (2008). Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology* 45(1), 141–150.

Blanco, G., Fargallo, J. A., Tella, J. L. & Cuevas, J. A. (1997). Role of buildings as nest-sites in the range expansion and conservation of choughs – *Pyrrhocorax pyrrhocorax* – in Spain. *Biological conservation* 79(2), 117–122.

Bruun, M. & Smith, H. G. (2003). Landscape composition affects habitat use and foraging flight distances in breeding European starlings. *Biological Conservation* 114(2), 179–187.

Buckingham, D. L. & Peach, W. J. (2005). The influence of livestock management on habitat quality for farmland birds. *Animal Science* 81(02), 199–203.

Burnham, K. P. & Anderson, D. (2010). *Model selection and multi-model inference*. 2nd. ed Springer. New York, USA.

Butler, S. J., Vickery, J. A. & Norris, K. (2007). Farmland biodiversity and the footprint of agriculture. *Science* 315(5810), 381–384.

Chamberlain, D. E. & Crick, H. Q. P. (1999). Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. *Ibis* 141(1), 38–51.

Chamberlain, D. E. & Fuller, R. J. (2000). Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystems & Environment* 78(1), 1–17.

Chamberlain, D. E., Wilson, A. M., Browne, S. J. & Vickery, J. A. (1999). Effects of habitat type and management on the abundance of skylarks in the breeding season. *Journal of Applied Ecology* 36(6), 856–870.

Chiron, F., Filippi-Codaccioni, O., Jiguet, F. & Devictor, V. (2010). Effects of non-cropped landscape diversity on spatial dynamics of farmland birds in intensive farming systems. *Biological Conservation* 143(11), 2609–2616.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I. & Tscharntke, T. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology* 44(4), 804–812.

Dallimer, M., Gaston, K. J., Skinner, A. M. J., Hanley, N., Acs, S. & Armsworth, P. R. (2010). Field-level bird abundances are enhanced by landscape-scale agri-environment scheme uptake. *Biology letters* 6(5), 643–646.

Davey, C. M., Vickery, J. A., Boatman, N. D., Chamberlain, D. E., Parry, H. R. & Siriwardena, G. M. (2010). Assessing the impact of entry level stewardship on lowland farmland birds in England. *Ibis* 152(3), 459–474.

Davey, C., Vickery, J., Boatman, N., Chamberlain, D., Parry, H. & Siriwardena, G. (2010). Regional variation in the efficacy of Entry Level Stewardship in England. *Agriculture, Ecosystems & Environment* 139(1–2), 121–128.

Donald, P. (2004). *The Skylark*. A&C Black, London, UK.

Donald, P. F., Sanderson, F. J., Burfield, I. J. & van Bommel, F. P. J. (2006). Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment* 116(3–4), 189–196.

Dänhardt, J., Green, M., Lindström, Å., Rundlöf, M. & Smith, H. G. (2010). Farmland as stopover habitat for migrating birds – effects of organic farming and landscape structure. *Oikos* 119(7), 1114–1125.

Eggers, S., Unell, M. & Pärt, T. (2011). Autumn-sowing of cereals reduces breeding bird numbers in a heterogeneous agricultural landscape. *Biological Conservation* 144(3), 1137–1144.

Erdos, S., Báldi, A. & Batáry, P. (2009). Nest-site selection and breeding ecology of Sky Larks Alauda arvensis in Hungarian farmland. *Bird Study* 56(2), 259–263.

Evans, K. L., Wilson, J. D. & Bradbury, R. B. (2007). Effects of crop type and aerial invertebrate abundance on foraging barn swallows *Hirundo rustica*. *Agriculture, Ecosystems & Environment* 122(2), 267–273.

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M. & Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14(2), 101–112.

Fuller, R. J., Hinsley, S. A. & Swetnam, R. D. (2004). The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis* 146, 22–31.

Gabriel, D., Carver, S. J., Durham, H., Kunin, W. E., Palmer, R. C., Sait, S. M., Stagl, S. & Benton, T. G. (2009). The spatial aggregation of organic farming in England and its underlying environmental correlates. *Journal of Applied Ecology* 46(2), 323–333.

Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E. & Benton, T. G. (2010). Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters* 13(7), 858–869.

Gillings, S., Newson, S. E., Noble, D. G. & Vickery, J. A. (2005). Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proceedings of the Royal Society B: Biological Sciences* 272(1564), 733–739.

Gilroy, J. J., Anderson, G. Q. A., Grice, P. V., Vickery, J. A. & Sutherland, W. J. (2010). Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland. *Ibis* 152(1), 90–104.

Gregory, R. D., G. Noble, D. & Custance, J. (2004). The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146, 1–13.

Gregory, R. D., Strien, A. van, Vorisek, P., Meyling, A. W. G., Noble, D. G., Foppen, R. P. B. & Gibbons, D. W. (2005). Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360(1454), 269–288.

Grüebler, M. U., Korner-Nievergelt, F. & Von Hirschheydt, J. (2010). The reproductive benefits of livestock farming in barn swallows *Hirundo rustica*: quality of nest site or foraging habitat? *Journal of Applied Ecology* 47(6), 1340–1347.

Haslem, A. & Bennett, A. F. (2008). Birds in agricultural mosaics: The influence of landscape pattern and countryside heterogeneity. *Ecological Applications* 18(1), 185–196.

Henderson, I. G., Cooper, J., Fuller, R. J. & Vickery, J. (2000). The relative abundance of birds on set-aside and neighbouring fields in summer. *Journal of Applied Ecology* 37(2), 335–347.

Hendrickx, F., Maelfait, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V. & Bugter, R. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology* 44(2), 340–351.

Herzon, I. & Helenius, J. (2008). Agricultural drainage ditches, their biological importance and functioning. *Biological Conservation* 141(5), 1171–1183.

Herzon, I. & O'Hara, R. B. (2007). Effects of landscape complexity on farmland birds in the Baltic States. *Agriculture, Ecosystems & Environment* 118(1–4), 297–306.

Hole, D. G., Perkins, A. J., Wilson, J. D., Alexander, I. H., Grice, P. V. & Evans, A. D. (2005). Does organic farming benefit biodiversity? *Biological Conservation* 122(1), 113–130.

Ihse, M. (1995). Swedish agricultural landscapes — patterns and changes during the last 50 years, studied by aerial photos. *Landscape and Urban Planning* 31(1–3), 21–37.

Jansson, U. [Ed] (2011). *Agriculture and Forestry in Sweden since 1900. A Cartographic Description.* Stockholm: Royal Swedish Academy of Agriculture and Forestry 2011 (National Atlas of Sweden), Stockholm, Sweden.

Jonason, D., Andersson, G. K. S., Öckinger, E., Rundlöf, M., Smith, H. G. & Bengtsson, J. (2011). Assessing the effect of the time since transition to organic farming on plants and butterflies. *Journal of Applied Ecology*.

Josefsson, J. (2012). *Biodiversity in agricultural landscapes [Elektronisk resurs] : causes, constraints and opportunities* [online]. Uppsala: Department of Ecology, Swedish University of Agricultural Sciences. Available from: http://urn.kb.se/resolve?urn=urn:nbn:se:slu:epsilon-e-327. [Accessed 2013-10-24].

Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E. J. P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T. M. & Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters* 9(3), 243–254.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G. & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution* 26(9), 474–481.

Kleijn, D. & Sutherland, W. J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40(6), 947–969.

Kragten, S. & de Snoo, G. R. (2008). Field-breeding birds on organic and conventional arable farms in the Netherlands. *Agriculture, Ecosystems & Environment* 126(3–4), 270–274.

Krebs, J. R., Wilson, J. D., Bradbury, R. B. & Siriwardena, G. M. (1999). The second Silent Spring? *Nature* 400(6745), 611–612.

Low, M., Arlt, D., Eggers, S. & Pärt, T. (2010). Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology* 79(1), 214–224.

Marshall, E. J. P., Brown, V. K., Boatman, N. D., Lutman, P. J. W., Squire, G. R. & Ward, L. K. (2003). The role of weeds in supporting biological diversity within crop fields. *Weed Research* 43(2), 77–89.

Morris, A. J. & Gilroy, J. J. (2008). Close to the edge: predation risks for two declining farmland passerines. *Ibis* 150, 168–177.

Morris, A. J., Holland, J. M., Smith, B. & Jones, N. E. (2004). Sustainable Arable Farming For an Improved Environment (SAFFIE): managing winter wheat sward structure for Skylarks *Alauda arvensis*. *Ibis* 146, 155–162.

Newton, I. (2004). The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146(4), 579–600.

Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Hart, B., Mathews, F., Macdonald, D. & Fuller, R. J. (2009). Consequences of organic and non-organic farming practices for field, farm and landscape complexity. *Agriculture, Ecosystems & Environment* 129(1–3), 221–227.

Orians, G. H. & Pearson, N. E. (1979). On the theory of central place foraging. *Analysis of Ecological Systems* (Ed. by D. J. Horn, R. D. Mitchell & G. R. Stairs), pp. 154-177. Ohio University Press, Ohio.

Pain, D. J. & Pienkowski, M. W. (1997). *Farming and birds in Europe: the common agricultural policy and its implications for bird conservation*. Academic Press, San Diego, USA.

Peach, W. J., Lovett, L. J., Wotton, S. R. & Jeffs, C. (2001). Countryside stewardship delivers cirl buntings (*Emberiza cirlus*) in Devon, UK. *Biological Conservation* 101(3), 361–373.

Pickett, S. R. A. & Siriwardena, G. M. (2011). The relationship between multi-scale habitat heterogeneity and farmland bird abundance. *Ecography* 34(6), 955–969.

Piha, M., Pakkala, T. & Tiainen, J. (2003). Habitat preference of the Skylark *Alauda arvensis* in southern Finland. *Ornis Fennica* 80, 97–110.

Piha, M., Tiainen, J., Holopainen, J. & Vepsäläinen, V. (2007). Effects of land-use and landscape characteristics on avian diversity and abundance in a boreal agricultural landscape with organic and conventional farms. *Biological Conservation* 140(1-2), 50–61.

von Post, M., Borgström, P., Smith, H. & Olsson, O. (2012). Assessing habitat quality of farm-dwelling house sparrows in different agricultural landscapes. *Oecologia* 168(4), 959–966.

Pärt, T. & Söderström, B. (1999). Conservation value of semi-natural pastures in Sweden: contrasting botanical and avian measures. *Conservation Biology* 13(4), 755–765.

Robertson, J. G., Eknert, B. & Ihse, M. (1990). Habitat analysis from infra-red aerial photographs and the conservation of birds in Swedish agricultural landscapes. *Ambio* 195–203.

Robinson, R. A., Wilson, J. D. & Crick, H. Q. P. (2001). The importance of arable habitat for farmland birds in grassland landscapes. *Journal of Applied Ecology* 38(5), 1059–1069.
Smith, H., Dänhardt, J., Lindström, Å. & Rundlöf, M. (2010). Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia* 162(4), 1071–1079.
Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzon, I., van Doorn, A., de Snoo, G. R., Rakosy, L. & Ramwell, C. (2009). Ecological impacts of early 21st century agricultural change in Europe – A review. *Journal of Environmental Management* 91(1), 22–46.
Stoate, C., Boatman, N., Borralho, R., Carvalho, C. R., Snoo, G. R. d. & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63(4), 337–365.
Suhonen, J., Norrdahl, K. & Korpimäki, E. (1994). Avian predation risk modifies breeding bird community on a farmland Area. *Ecology* 75(6), 1626–1634.
Sveriges Ornitologiska Förening (2013). Rädda Sånglärkan. http://www.sofnet.org/radda_sanglarkan [2013-11-01]
Swedish Board of Agriculture (2013). Mångfald på slätten. http://www.jordbruksverket.se/amnesomraden/miljoklimat/ettriktodlingslandskap/mangfaldpaslatten.4.e01569712f24e2ca09800012316.html [2013-11-01]
Söderström, B. & Pärt, T. (2000). Influence of landscape scale on farmland birds breeding in semi-natural pastures. *Conservation Biology* 14(2), 522–533.
Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8(8), 857–874.
Tucker, G. M. & Evans, M. I. (1997). *Habitats for birds in Europe: A conservation strategy for the wider environment*. BirdLife International. Cambridge, UK.
Vepsäläinen, V., Tiainen, J., Holopainen, J., Piha, M. & Seimola, T. (2010). Improvements in the Finnish agri-environment scheme are needed in order to support rich farmland avifauna. *Annales Zoologici Fennici* 47(October), 287–305.
Whelan, C. J., Wenny, D. G. & Marquis, R. J. (2008). Ecosystem Services provided by birds. *Annals of the New York Academy of Sciences* 1134(1), 25–60.
Whittingham, M. J. (2007). Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied ecology* 44(1), 1–5.
Whittingham, M. J. (2011). The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology* 48(3), 509–513.
Whittingham, M. J., Krebs, J. R., Swetnam, R. D., Vickery, J. A., Wilson, J. D. & Freckleton, R. P. (2007). Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecology Letters* 10(1), 25–35.
Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology* 75(5), 1182–1189.
Whittingham, M. J., Wilson, J. D. & Donald, P. F. (2003). Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. *Ecography* 26(4), 521–531.

Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A. & Grice, P. V. (2004). The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation* 119(1), 19–39.

Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J. & Brown, V. K. (2001). The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38(3), 647–664.

Vickery, J., Carter, N. & Fuller, R. J. (2002). The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agriculture, Ecosystems & Environment* 89(1–2), 41–52.

Wilson, J. D., Evans, J., Browne, S. J. & King, J. R. (1997). Territory Distribution and Breeding Success of Skylarks *Alauda arvensis* on Organic and Intensive Farmland in Southern England. *Journal of Applied Ecology* 34(6), 1462–1478.

Wilson, J. D., Morris, A. J., Arroyo, B. E., Clark, S. C. & Bradbury, R. B. (1999). A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems & Environment* 75(1–2), 13–30.

Wilson, J. D., Whittingham, M. J. & Bradbury, R. B. (2005). The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? *Ibis* 147(3), 453–463.

Virkkala, R., Luoto, M. & Rainio, K. (2004). Effects of landscape composition on farmland and red-listed birds in boreal agricultural-forest mosaics. *Ecography* 27(3), 273–284.

Wretenberg, J., Lindström, Å., Svensson, S. & Pärt, T. (2007). Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. *Journal of Applied Ecology* 44(5), 933–941.

Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. & Pärt, T. (2006). Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology* 43(6), 1110–1120.

Wretenberg, J., Pärt, T. & Berg, Å. (2010). Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. *Biological Conservation* 143(2), 375–381.

Zuur, A. F., Savaliev, A. A. & Ieno, E. N. (2012). *Zero Inflated Models and Generalized Linear Mixed Models with R*. Highland Statistics Ltd., Newburgh, UK.

Öberg, M., Pärt, T., Arlt, D., Laugen, A. T. & Low, M. (2013). Decomposing the seasonal fitness decline. *Oecologia* DOI:10.1007/s00442-013-2763-z.

Acknowledgements

Supervisors

Tomas P, I will never forget the day we first calculated the number of data sheets that would be needed for this project (something like $2_{\text{survey types}} \times 20_{\text{sites per landscape}} \times 5_{\text{visits per site}} \times 40_{\text{landscapes}}$). You didn't bat an eyelid, I felt like crying and going back to my old job at Länsstyrelsen. I am still amazed by your vision and belief that we could pull such a huge project off. Some things worked, some didn't but I can honestly say this has been an incredible journey filled with tears, joy and laughter, and I've learnt a thing or two as well! Thanks for pushing me and always being available for a chat.

Åke B, one foot in science and the other in muddy fields. Your ideas, supervision and innate calmness have been essential during all stages of this enormous undertaking of a project. Thanks!

Sönke E, you haven't been involved with so many "official" supervisor meetings, but it is probably you I have talked with most about farmland birds. In coffee rooms, in cars, in bars, in hotels; just mention the word skylark and we're off; much to the disgust of some colleagues. Thanks for your inspiration and passion for our subject area.

Åsa B, the importance of having a supervisor on the periphery of this project cannot be stated enough. Your pertinent questions regarding things I (and the others) just took for granted has made me re-think things and realise how easy it is to be blinded by my own perspectives. Thanks for your input!

Unofficial supervisor

Matt L, thanks for always being there! Stats, texts, databases, programming; you name it you've helped with it more or less during my time as a PhD student.

Assistants

Thanks for putting up with a new PhD student who was trying to get almost 40 people (most of who he still has never met) to do exactly as he wanted (for the sake of data quality) mostly via email. It seems like a long time ago now, but I am sure our lives felt empty when my emails stopped after the breeding season of 2009. So in absolutely no particular order thanks to: Mikael R, Oskar N, Jan H, Janne D, Juliana D, Kaj S, Mattias U, Olof J, Urban M, Henrik B, Mats W-P, Nils-Olof J, Pekka W, Claes T, Ingemar H, Karin G, Lars-Ove N, Gun-Britt E, Sture H, Stefan H, Daniel I, Sven O, Albin L, Erik F N, Jan R, Agnetha A, Anders B, Anders E, Anders G, Anders O (are all the men in Östergötaland called Anders? Strange!), Arne E, Christer I, Ingvar C, Pål K, Ulrika R. I hope I haven't forgotten anyone.

A very special thanks go to the people involved in pre bird season planning. Emilia B, Linda G, Frida N and Marianne M. I think we are the only ones who really know the amount of work that went into those winter land use surveys, GIS work and farmer contacts. And I still remember the day we nearly lost it all (twice?)! Thanks again.

PhDs past and present

Jens Å, thanks for not being offended by all of the swearing while I was first learning R. And thanks for showing me the advantages of persevering with it. I have no doubt that conversations with you (and Matt) influenced the direction my PhD work took. Thanks for not getting annoyed with me (at least not overtly) during all of the phone calls to our office in the beginning.

Viktor J, being in your company made me feel thirty again, or 25 depending on how old you really are. I will always remember Argentina. Thanks for all the fun!

Måns S, you are of course my partner in cynicism (when we were feeling cynical, which wasn't always). I think in many ways we have shared similar experiences during our PhD time, especially because we have children of roughly the same age. I have appreciated our chats during this period!

Johanna L, thanks for being able to talk about life as a Phd student, model selection, ecology, kids and football, almost the only subject areas that I have been able to talk about recently.

Jonas J, life in our research group became more interesting for me when you joined. Our "gödselklubb" meetings were inspiring for both newer and older research ideas.

Camilla W, thanks for your help in the beginning of my time at SLU. You seemed to always know who to contact about stuff, either PhD related or farmland stuff (if you didn't know the answers yourself that is).

Maria N, your level of organisation is amazing. I am just happy we didn't share a room. We haven't seen each other much the last couple of years because of our respective parental leaves. I have missed our chats.

Diana R, thanks for all the fun while working on the legendary "Weaver Paper" both in the field and back at SLU.

All other colleagues at the Department of Ecology, Thanks for all discussions serious or otherwise!

Family

Sarah, there is no doubt whatsoever that the trajectory of my life changed the day you walked up that gangplank nearly a life time ago. And here we are. Thanks for being understanding and supportive when the home-life work-life balance hasn't always swung in your favour. I couldn't have done this without your sacrifices and help.

Tilde, Jakob and Liv, you are my inspiration. Love you!

Mum, I left home so many years ago. Now I have lived most of my adult life (all of it really) abroad and miles away from you. We don't see each other nearly enough, but I owe you so much. Thanks for everything mum!

Dad, I am where I am because as a child you gave me an interest in the natural world. That interest has taken me places that I know you could have only dreamed of visiting during your life. Thanks for believing in me, even when I sometimes made it hard for you to do so.

Steve and Lorna, we currently have nine children between us and live in different countries. We don't see each other enough!!! But who can blame us. I believe we are still close in other ways, even if not in physical distance and I hope this never changes.

Sarah's family (both close and extended), your support, hospitality and caring has more than helped me since moving to Sweden many years ago. Thanks!

Others

Jose Luis R, I am an ecologist working with bird conservation because I stumbled across you in a small cloud-forest reserve way back in 2001 and you inspired me. Thanks!

Sven Olof O, I would not have been able to realise my dream of becoming a biologist without the work you gave me when I first moved to Sweden many, many years ago. Thanks for everything. Who knows, I might be back in the workshop soon, although I hope not.

Jochen W and Anders B, thanks for the birding trips. All were well needed breaks during this PhD period (even if I was probably subconsciously counting skylarks, starlings and yellowhammers instead of looking for the more "exciting" stuff). Anders you were there when Sarah went into Labour with Tilde, and Jochen you were with us when Liv was born on the street in the middle of the night. Great birding buddies and midwives as well, can't be bad. Thanks!

Old colleagues from "Länsstyrelesen", it was sad to leave five years ago, but the knowledge I took with me has helped immensely during my PhD time.

Old friends and teachers from Umeå University and Gothenburg University, you fuelled my enjoyment for learning about biology and especially evolution, ecology and conservation. Thanks!